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## SPECIATION IN THE *AGATHYMUS* (Megathymidae)

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I CAN REMEMBER BACK in the past when we used to collect butterflies with a net and killing jar and then there were fifteen recognized species in two genera in the family Megathymidae. Today we have 47 species in five genera in that family and the net has long since been retired after we discovered that it was much more efficient to collect these "critters" with a fox hole pick, drain spade or sharp knife. Once when we had available a few hundred specimens of these insects the taxonomy seemed comparatively simple, and now that we have several thousand specimens available for study complications present themselves.

In making a study of speciation in the *Agathymus* we must recognize a number of species complexes that exist in that genus. They are the *neumoegeni*, *chisosensis*, *hoffmanni*, *evansi*, *aryxna*, *baueri*, *alliae*, *stephensi*, *polingi*, *mariae*, *remingtoni*, *rethon*, and *indecisa* complexes. Of these the following are very complicated and indicate a considerable amount of evolution is in progress: *neumoegeni*, *hoffmanni*, *aryxna*, *mariae*, and *remingtoni*, and it is with this group that I would like to go into with some detail.

*Agathymus* speciation particularly in the *mariae* complex has intrigued me for a number of reasons, one of which has been the method by which new species apparently developed during the past ages from a *mariae*-like prototype. In making a detailed study of this species complex in the United States a number of very interesting observations were encountered some of which I would like to discuss briefly. One of the first things that was noticed about *mariae* was its close association with its larval food plant *Agave Lecheguilla* Torr. During the number of

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years that I have collected *mariae* and other related species I have never found a specimen in any other species of *Agave* other than members of the *lecheguilla* complex, with the possible exception of a Mexican species that feeds in *Agave falcata* Engelm. Indications are that at one time *lecheguilla* occurred extensively from the Edwards Plateau in Texas over into New Mexico and well down into Mexico. Fossil seeds have been found in areas of Texas now completely devoid of these plants. In this vast expanse a prototype of our modern species was well established with a gene pool common to all areas. Conditions arose resulting in the eradication of *lecheguilla* plants in many sections of this great area thus disrupting the gene pool. During the many years that followed mutations occurred in the restricted populations resulting in the production of individuals that differed from the original species. These isolated populations gradually changed both biologically and morphologically into five separate species in the Texas area. *Mariae* was the first described in this complex and it was found at El Paso, in the Franklin Mountains, and for many years was considered to be the only species present all over southwestern Texas. After carefully studying specimens from 32 locations in Texas and New Mexico it was found that there was actually five different species going under the name of *mariae*. *Chinatiensis* Freeman, in the Chinati Mountains and near vicinity; *lajitaensis* Freeman, in the Lajita region of the Big Bend; *rindgei* Freeman, and *gilberti* Freeman, in the general vicinity of Del Rio; and *mariae* (B. & B.), from the Big Bend and McCamey regions westward and north to Carlsbad, New Mexico and El Paso, Texas. In no area do more than two of these species occur together and when this happens it was found that they have changed somewhat their larval feeding habits. In the Boquillas Canyon, Dryden, and Langtry areas where *gilberti* and *mariae* fly together, *gilberti* larvae penetrate into the caudex of the plant to a depth of 20 mm, whereas *mariae* does not penetrate more than 5 mm into the caudex, but does most of its feeding in the lower portion of the leaves. In the Del Rio, Juno, and Bracketville areas where *gilberti* and *rindgei* fly together *gilberti* penetrates sometimes to a depth of 30 mm into the caudex, whereas *rindgei* seldom penetrates below 20 mm. It is not unusual to find these two species and *estelleae* (Stallings & Turner) feeding in the same plant, each with a somewhat different feeding level, with *estelleae* feeding only in the leaves, *rindgei* the base of the leaves and upper caudex, and *gilberti* in the lower base of the leaves and deeper into the caudex. A rea-

sonable explanation for this is the rapidly declining population of *lecheguilla* plants in this general area, thus resulting in greater competition for food among these insects. The pH of the soil has considerable bearing on the occurrence of these species in a given habitat. *Mariae* is associated with distinctly alkaline soil, often from 7.7-8 pH; *chinatiensis* and *lajitaensis*, with soil somewhat less alkaline, around pH 7.2-7.4; and *gilberti* and *rindgei*, in soil that is neutral or only slightly alkaline, pH 7-7.1.

An interesting observation was made concerning the feeding habits of the larvae of *Aegiale hesperiaris* (Walker) and *Agathymus hoffmanni* (Freeman) in *Agave americana* L. in Mexico. In areas where *hoffmanni* is fairly abundant, especially in the valley of Mexico, the larvae feed in a small species of a parryi-like *Agave*, and overlook the larger *americana* plants, in which the larvae of *hesperiaris* are found. The *hoffmanni* trap doors are located on the lower surface and usually near the center of the leaf. In areas where both species are found in the same plant, some member of the *americana* complex, *hoffmanni* prefer the hip of the leaf for their feeding area leaving the center portion for the much larger *hesperiaris* larvae, or else the *hesperiaris* forced them into that position. Specimens of *hoffmanni* from these areas are atypical, indicating that they have evolved or else are in the process of evolving into a separate species. Both biological and morphological work on these specimens is difficult due to the scarcity of the individuals. When sufficient material is present for study it may then be possible to determine the exact status of these *hoffmanni*-like specimens.

In Arizona some parallel evolution appears to be present in various populations of *Agathymus aryxna* (Dyar). In the general area of the Chiricahua Mountains southward through Ramsey Canyon or into northern Mexico is found one population with similar characteristics. Another population begins near Globe and extends through Santa Catalina, Rincon, and Santa Rita Mountains southward through the Patagonia Mountains into Sonora, Mexico. The third is a rather variable population that occurs in the Baboquivari Mountains and possibly on southward into Mexico. Indications are that at one time this entire area was covered with a *palmeri*-like *Agave* in which fed an *aryxna*-like prototype of our modern species. Environmental conditions plus man made factors eliminated the *Agave* in large areas thus producing desert and mountain islands where the plants are still undisturbed. Individuals from each population may be recognized by the width of the spots on both wings.

Starting with the eastern population, the spots are generally separate and fairly small. In the central population, the spots are somewhat larger and tend to be closer together. While in the western population, the spots are the largest, tending to fuse together in some cases. To me there seems no doubt that we are seeing evolved three separate subspecies that eventually will assume specific status within a number of years.

In the *neumoegeni* complex we have a number of so called species that exhibit characteristics indicating a common ancestor. Possibly some of these have evolved farther than others and are specific, however others may still be in the process of changing from distinct subspecies into full species. The test of breeding has just started to be worked upon by Stallings, Turner & Stallings and the results will likely be very conclusive in forming our conception of this complex. I have collected larvae of wild hybrids of a cross between male *mariae* and female *judithae* (Stallings & Turner), as well as the same in a cross between male *mariae* and female *diabloensis* Freeman and the resulting  $F_1$  did not resemble each other as much as the pure *judithae* and *diabloensis* do, especially the females. In all of the wild hybrids that I have seen to date involving *mariae* with some species of the *neumoegeni* complex it has always been the males of *mariae* that have resulted in the hybrids. This is based on the presence of the larvae in species of *Agave* other than members of the *lecheguilla* complex. From all evidence presented these  $F_1$  are sterile.

Two members of the *neumoegeni* complex are associated with juvenile plants, *neumoegeni* (Edwards) and *florenceae* (Stallings & Turner). All other species are associated with mature plants running from small to large in size. *Florenceae* and *neumoegeni* morphologically resemble each other more closely than do any of the other species in this group even though there is a great distance separating them in their distribution. Genetically speaking the entire complex is closely related.

In the *remingtoni* complex we have three described species, *remingtoni* (Stallings & Turner), *estelleae* (Stallings & Turner) and *comstocki* (Harbison), and several undescribed species. Genetically they are related, biologically they are very different. *Remingtoni* is found in the mountains in very rugged terrain, often on cliffs, with the pH on the acid side, and feeding upon a member of the *lecheguilla* complex. *Estelleae* is associated with alkaline or near neutral soil, usually in the plains country or else

where it is slightly hilly, and feeding upon another member of the *lecheguilla* complex. *Comstocki* is found in hilly, desert, areas of Baja California (pH has not been checked), feeding upon *Agave shawii* Engelm., which is not at all related to *lecheguilla*. The general range of *remingtoni* is Victoria, Tamps., Mexico southward to the Jacala, Hidalgo, area, while *estelleae* occurs north and west of Victoria. All indications point to a common ancestor of these two species that occurred in an area where the gene pool was available for all regions of the range. Due to environmental changes, both man made and natural, the gene pool was disrupted, eventually resulting in the formation of separate subspecies and eventually species.

In conclusion I would say that in the genus *Agathymus* we have had three major prototype complexes, the *neumoegeni*, *aryxna*, and *mariae*, and from these three all of our present day species evolved.

## REFERENCES

- COMSTOCK, JOHN A., 1957. Notes on the metamorphosis of an *Agave* boring butterfly from Baja California, Mexico. *Trans. San Diego Soc. Nat. Hist.* 12: 263-276, pl. 22.
- EDWARDS, W. H., 1882. Description of species of butterflies taken in Arizona by Jacob Doll, 1881. *Papilio* 2: 19-29.
- FREEMAN, H. A., 1950. Notes on *Megathymus*, with the description of a new species. *Field & Lab.* 18: 144-146.
- 1951a. Notes on the *Agave* feeders of the genus *Megathymus*. *Field & Lab.* 19: 26-32.
- 1951b. Ecological and systematic study of the Hesperioidea of Texas. *So. Methodist Univ. Studies*, no. 6:1-64.
- 1952. Two new species of *Megathymus*. *Amer. Mus. Novitates*, no. 1593:1-9, figs. 1-13.
- 1955. Four new species of *Megathymus*. *Amer. Mus. Novitates*, no. 1711: 1-20, figs. 1-34.
- 1958. A revision of the genera of the Megathymidae, with the description of three new genera. *Lepid. News.* 12: 81-92, 1 pl.
- 1960. Notes on *Agathymus* in Texas, and the description of a new species from Mexico (Megathymidae). *Journ. Lepid. Soc.* 14: 58-62.
- 1962. A new species of *Agathymus* from Texas. *Amer. Mus. Novitates*, no. 2097: 1-7, figs. 1-6.
- 1963. Type localities of the Megathymidae. *J. Res. Lep.* 2 (2): 137-141.

- \_\_\_\_\_ 1964a. The effects of pH on the distribution of the Megathymidae. *J. Res. Lep.* 3 (1): 1-4.
- \_\_\_\_\_ 1964b. Four new species of *Agathymus* from Texas. *Journ. Lepid. Soc.* 18: 171-185, 4 pls.
- \_\_\_\_\_ 1964c. Larval habits of *Agathymus mariae* (B. & B.). *J. Res. Lep.* 3 (3): 145-147.
- HARBISON, C. F., 1957. A new species of *Megathymus* from Baja California, Mexico. *Trans. San Diego Soc. Nat. Hist.*, 12: 231-262, pls. 18-21.
- \_\_\_\_\_ 1963. A second new species of megathymid from Baja California, Mexico. *Trans. San Diego Soc. Nat. Hist.*, 13: 61-71, 4 pls.
- STALLINGS, DON B. & J. R. TURNER, 1954. Notes on *Megathymus neumoegei* with description of a new species. *Lepid. News.* 8: 77-87.
- \_\_\_\_\_ 1957. Four new species of *Megathymus*. *Ent. News.* 68: 1-17.
- \_\_\_\_\_ 1958. A revision of the Megathymidae of Mexico, with a synopsis of the classification of the family. *Lepid. News.* 11: 113-137, 8 pls.
- \_\_\_\_\_ 1960. A new species of *Agathymus* and a new subspecies of *Megathymus*. *Ent. News.* 71: 109-115
- STALLINGS, DON B., J. R. TURNER & VIOLA N. STALLINGS, 1961. A new subspecies of *Agathymus mariae* from Mexico. *Journ. Lepid. Soc.* 15: 19-22.